Escape Responses of North Borneo Strombid Gastropods Elicited by the Predatory Prosobranchs *Aulica vespertilio* and *Conus marmoreus*

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INTRODUCTION

Active responses of prosobranch snails to potential predators, different from their normal slow and limited activity, caught the notice of biologists long ago. Most of the early work on this phenomenon was directed toward identification of the nature of the stimulus which elicited the response rather than to the role the response might play in the life of the snail possessing it. Thus, Hoffman (1930) demonstrated that the escape response in *Nassarius reticulatus* (Linnaeus, 1758) was normally mediated by chemoreception of some material from the asteroid predator, but that it could also be readily induced by artificial chemical, thermal and electrical means. The specificity of these behavioral patterns was further demonstrated by Bullock (1953) and Margolin (1964a, b) and the chemosensory basis of detection of the predator further confirmed. From these studies emerged the ideas that these behavior patterns elicited by chemosensory recognition of specific substances emanating from predators might serve in nature as avoidance or flight reactions to the presence of the predator and would therefore be of selective advantage to those species possessing them.

The lack of information on the effectiveness of these escape reactions upon spontaneous predator-prey confrontations in nature was partially filled by the field observations of Clark (1958) and Robertson (1961). Later, Gonor (1965) concluded that since the avoidance behavior had been observed to permit some individuals to successfully escape from attack by the predator, such behavior had selective advantage for the species and was thus adaptive. Consideration of the behavior of both the prey and predator led to the further conclusion that the common characteristics of the known escape reactions in marine invertebrates indicate that these behavior patterns are successfully evolved by normally slow moving prey species which are able to detect only by chemosensation the presence of a predator, itself slow moving and hunting its prey by chemosensation.

This study presents observations on the behavior of another set of predator and prey species which support and further illustrate conclusions previously reached, and add to the information available about the feeding habits of the predatory species involved. Two predatory gastropods, a cone and a volute, were observed to capture and eat two species of *Strombus*, which exhibited escape reactions when confronted with them.

OBSERVATIONS

These observations were made during February, 1965, on Cruise 6 of Stanford University's *Te Vega* Expeditions, during a stop at the islands Pulau Gaya and Pulau Mantabuan (118° 45′ E, 4° 36′ N) in Darvell Bay, North Borneo. Wide shallows of clean coral sand bottoms, with scattered Thalassia clumps, lie just off coral sand beaches inshore from the fringing reefs of these islands. Among the most commonly found snails of these shallow areas were two species of *Strombus*. Most abundant of the two was *S. gibberulus* Linnaeus, 1758 which was often found in groups. The slightly larger *S. luhuanus* Linnaeus, 1758 was also readily obtained in numbers although it was not as common as *S. gibberulus*. Both of these species are

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common in shallow water throughout the West Pacific (Abbott, 1960). *Lambis lambis* (Linnaeus, 1758), another strombid with wide Pacific distribution, was also available in this area and some observations were made on it. Two large predaceous gastropods, *Conus marmoreus* Linnaeus, 1758 and *Aulica vespertilio* (Linnaeus, 1758) were also found in this habitat. Both are common Indo-Pacific species.

REACTIONS OF *Aulica vespertilio* *Strombus gibberulus* AND *Strombus luhuanus*

During the middle of the day *Aulica vespertilio* is found ploughing along just under the surface of the sand, and also occasionally on the surface. Some individuals were found under the sand holding a Strombus in the foot and feeding on it. On one occasion, a group of five Aulica were found in a tight cluster. When the group was examined, it was found that in the center there was an Aulica holding and feeding upon a small Strombus. The other volutes were also attempting to feed upon the animal originally captured by the center one, having been attracted to the site where the prey was being eaten. It was evident that extensive predation on the Strombus populations by this and possibly other predators was taking place, for large numbers of fresh shells of *Strombus luhuanus* in good condition and not bored were found in several places, scattered about the bottom in about 2 meters of water in an area where *Conus marmoreus* was also found.

Observations on the capture of *Strombus gibberulus* by *Aulica vespertilio* were made on a level coral sand area in the late afternoon, as a rising tide began to cover the higher areas of the flat near the beach. A number of large *A. vespertilio* were seen in this area, moving about on the sand bottom in water about 10 cm deep. *Strombus gibberulus* was abundant in scattered groups. and appeared to be just emerging from the sand as the tide rose over the area. When the movements of the Aulica brought them near groups of Strombus, they quickened their crawling and moved rapidly toward the strombs. Upon approaching the prey, the Aulica fully extended the foot, raised the head and anterior end of the shell, extended the siphon which had been pointing directly ahead and began to swing it from side to side. When an Aulica came close to a Strombus, it spread the propodium of the foot out wider, lifted it high above the sand and with a forward thrust brought it down quickly. If the Strombus was missed, as it often was on the first attempt, the volute quickly tried the "pouncing" action to each side several times. When groups of Strombus were approached within about 15 cm by a volute, all of them quickly came out of the sand, and became very active, moving away by quick kicks of the foot until they were about 30 cm away. The volutes pursued the strombs, and often caught them, but the violent kicking by the strong foot of the Strombus usually broke the hold of the volute, especially if the foot of the stromb was turned to work against the foot of the volute. The captured strombid often upset its much larger captor and escaped by continuing to kick while the volute attempted to right itself. When a pounce was successful the Aulica quickly began to manipulate the prey so that it was held longitudinally in the foot, but even when the Aulica partially enveloped the strombid, the foot of the latter is strong enough so that its violent kicking can sometimes break the hold before the volute can completely envelop it.

Capture was observed in more detail by repeatedly placing the two species together in pans until the pattern of behavior was understood. Freshly collected *Strombus gibberulus* and *S. luhuanus* were placed in sea water in a plastic pan with sand on the bottom to permit normal locomotion. After the strombids had stopped moving and assumed their normal position, slightly sunk into the sand, a large *Aulica vespertilio* (shell length approximately 10 cm) from the group found hunting in the field the same day was placed in the center of the pan. In a few seconds, most of the strombids had begun to move, kicking more quickly and more violently than during normal locomotion or righting. After 10 minutes, the strombids not near the volute had stopped kicking, but those in its immediate vicinity continued to exhibit vigorous escape reactions, usually orienting themselves with the anterior end away from the volute before kicking themselves forward. The volutes began to pursue the strombids around the periphery of the pan and frequently caught them, but as in the field the hold was sometimes broken. When finally a volute obtained a firm grasp with the propodium on the shell of a Strombus, it transferred the prey along the length of the foot to the posterior trailing portion. This part of the foot was then expanded, enveloping the strombid in a pocket formed by stretching above the snail and contracting around it below. The volutes then carried the enclosed strombid, which formed a large bulge in the top of the posterior portion of the foot, around for some hours. Subsequent feeding was not observed, but partially eaten Strombus were regularly found in the pans the next morning when the volutes were left overnight with the Strombus. Cannibalism does not occur when the Strombs, which are herbivorous (Robertson, 1961), are kept together alone.

REACTIONS OF *Conus marmoreus* AND *Strombus* spp.

Conus species feed at night (KOHN, 1959) and consequently predation on Strombus by this species was not observed in the field. At Pulau Gaya, during the day, *C. marmoreus* was found buried, quiescent, beneath the sand. Simple experiments similar to those performed with *Aulica vespertilio* were carried out to determine if this cone would capture and eat Strombus and to observe the reaction of Strombus to the presence of the cone. Typical experiments are described below; the results were readily repeatable. Animals were collected the same day they were used.

Eight *Strombus gibberulus* and three *S. luhuanus* were placed in a plastic pan (28 x 35 cm) in sea water three inches deep with the bottom covered with clean coral sand to permit normal locomotion. After some locomotory activity the animals became quiet, and evenly distributed over the bottom of the pan. A large *Conus marmoreus* (13 cm shell length) was then placed in the center of the pan with the Strombus, several of which became very active in a few seconds. Within one minute all individuals had become very active, moving rapidly and erratically about the pan by their strong kicking action. This activity did not depend upon contact with the cone but was stimulated by proximity. The cone was removed from the pan after two minutes but the activity continued, and did not subside until the water in the pan had been replaced with fresh sea water several times.

The chemical nature of the sensory clue to the presence of the cone for the Strombus was demonstrated by another simple experiment. Fresh sea water slowly added to a bowl containing four quiet *Strombus gibberulus* caused no locomotory activity. However, when 200 ml of sea water in which a live *Conus marmoreus* had been kept for two hours was poured slowly into the bowl containing the four Strombus in 50 ml of sea water, the strombids began immediately to kick violently. There was also no response when fresh sea water was poured into a pan containing 20 *S. gibberulus*. When 200 ml of water in which a *C. marmoreus* had been kept for two hours was slowly poured into at least 8 times its volume of sea water in the pan all the Strombus began kicking strongly in a few seconds. This activity continued for five minutes; the activity subsided after the water in the pan was repeatedly changed.

In an attempt to study the hunting activity of *Conus marmoreus* at twilight (6 PM in February) ten *Strombus gibberulus* were placed in a plastic pan of sea water with sand on the bottom. A large *C. marmoreus* (10 cm long) was placed in the pan, causing all of the Strombus to react strongly within a few seconds. After 10 minutes the Strombus had become quiet again and the cone had begun to move slowly through the sand. Individual Strombus resumed activity and leaped away whenever closely approached by the cone. Capture of a Strombus by *C. marmoreus* was not seen during observation of this experiment and subsequent repetitions. However, on this and two other occasions when cones were left overnight in the pans with the *S. gibberulus*, capture and feeding occurred unobserved. The following morning the cone was found partially buried in the sand and one of the Strombus was found dead, with the muscular portions of the body eaten away. The cones were very sensitive to light and were found fully expanded and active in the pans only at night, after the pans had been in darkness and covered for some hours.

REACTION OF *Lambis lambis* TO *Conus marmoreus* AND *Aulica vespertilio*

Lambis lambis, a strombid very much larger (shell length over 15 cm) than the adult *Strombus gibberulus* (shell length ca. 5 cm) and the *S. luhuanus* (shell length ca. 6 cm) was also common in the vicinity of Pulau Gaya, and its reaction to *Aulica vespertilio* and *Conus marmoreus* was tested. *Lambis lambis* is a very sedentary animal, remaining motionless for long periods when placed in pans of sea water. When an *A. vespertilio* was placed in a pan of sea water containing four *L. lambis* resting on a sand layer, limited kicking by the *Lambis*, sufficient to move them a short distance, occurred. When a *C. marmoreus* was placed in a pan with the large *Lambis*, a more vigorous reaction was produced. The long, thin foot was extended fully and the *Lambis* moved themselves about in the pan by strong thrusts. No predation occurred when *Aulica* and *Conus* were left overnight in the pans with the *Lambis* and none was observed in the field.

ESCAPE REACTIONS IN THE STROMBIDAE

DISCUSSION

Escape reactions in the Strombidae were first noticed by ROBERTSON (1961) who found that a marked escape reaction was evoked in adult and young *Strombus gigas* LINNAEUS, 1758, *S. costatus* GMELIN, 1790 and *S. raninus* GMELIN, 1790 by the presence of *Fasciolaria tulipa* (LINNAEUS, 1758). This carnivorous prosobranch was found by ROBERTSON to be an important predator of young *Strombus* spp. at Bimini. RANDALL (1964) also observed predation of young *S. gigas* by *F. tulipa* at St. Johns, West

Indies. The present study demonstrated that *S. gibberulus* and *S. luhuanus*, both small species are also subject as adults to predation by two carnivorous prosobranchs.

It is probable that adults of *Strombus gigas* and other large strombids such as *Lambis lambis* cannot be captured by predatory snails smaller than themselves even though such species still show an escape reaction as adults to such predators. In these large Strombidae, the escape reaction would therefore be of greatest importance for survival during the juvenile stages, when predatory gastropods are able to capture the smaller individuals. Escape reactions to prosobranch predators would be of minor survival value for the adults of these large snails which are being subjected to greater predation by swift moving predators hunting by sight. RANDALL for example found that the principal predators of *S. gigas* were hermit crabs, spiny lobsters, loggerhead turtles and 15 species of fish (*op. cit.* 1964). It was previously indicated (GONOR, 1965) that the known gastropod escape reactions would be ineffective with predators of this type.

The snail predators are able to capture adults of the smaller species studied in this investigation, and the escape reaction, shown by field observations to be effective, is correspondingly more important as a survival mechanism throughout the lives of these Strombus species even if they are preyed upon by other types of predators. The conclusion previously reached (GONOR, 1965) that gastropod escape reactions are functional, i. e. of selective advantage, and are evolved as an adaptive response to predation by slow moving predators hunting by chemosensation is upheld.

Speculation on the mode of origin of gastropod escape reactions is inviting since the reality of their selective advantage is now well supported. A common feature of the mechanisms employed by most gastropod species in escape behavior is that they involve both anatomical and behavioral features used normally in locomotory activities and in righting, except that these actions are used at an accelerated pace to escape a slow moving predator. The locomotory responses of limpets and turban snails to starfish are more striking in their rapidity than in their uniqueness. The mantle response of *Diodora aspera* ESCHSCHOLTZ, 1833 and the Naticids (MARGOLIN, 1964a) is a more specialized behavior but the ability to cover parts of the shell with the pallium is common in gastropods. Nassarids are very active snails and use the same actions for righting, rapid locomotion when roughly handled, and in escape reactions. GORE (1966) discusses this similarity in *Nassarius vibex* (SAY, 1822) in detail.

In *Strombus* the similarity of the normal locomotory activity (PARKER, 1922) and that elicited by the predator is obvious; they differ only in the frequency and strength of the leaping. ROBERTSON considered that the leaping of strombs was principally related to escape from predators. However, when the escape behavior of other prosobranchs is considered it seems more probable the behavior employed in avoidance reactions was not evolved *de novo,* but developed from pre-existing locomotory mechanisms.

It would seem that the most significant and novel feature evolved in the development of these reactions was not the movements, for they are also part of basic activities, but the acquisition of the sensory basis for detection and discrimination of a substance emanating from the predator. BULLOCK (1953) noted that the specific adaptive behavior of the prey species indicated remarkable recognition of the predator, and subsequent experimentation (MARGOLIN, 1964a, b, GORE, 1966) has only further demonstrated how specific and sensitive this can be. Escape reactions then might be viewed as primarily not a new behavioral adaptation but rather a new sensory one coupled to an existing behavioral pattern capable of acceleration.

Despite an initial marked response to the presence of *Aulica* and *Conus* both *Strombus gibberulus* and *S. luhuanus* eventually ceased to respond to their continuing presence, except when contacted more closely. This type of drop off is characteristic of gastropod escape reactions under artificial circumstances. Ultimate cessation of the response upon repeated stimulation was observed by both BULLOCK (1953) and MARGOLIN (1964a, b).

FEEDING HABITS OF *Conus marmoreus* AND *Aulica vespertilio*

Species of the genus *Conus* are specialized predators usually feeding on one type of prey, and may be divided into groups according to whether they feed upon fish, worms or snails. ENDEAN (1963) demonstrated that the feeding specificity is correlated with differences in the toxic and paralytic properties of the cone venoms. In general, the venoms were found to be effective only on members of the group upon which the species of *Conus* normally feed. The venom of *Conus marmoreus* was found to be toxic to gastropods and also to produce a flaccid paralysis in them. KOHN (1959) found that on Hawaii *C. textile* LINNAEUS, 1758, *C. pennaceus* BORN, 1778 and *C. marmoreus* fed upon gastropod species, the latter two exclusively. He remarked that the most striking aspect of the food of *C. marmoreus* was that it appeared to consist entirely of other species of *Conus*. However, *C. marmoreus* is at the limit of its range at Hawaii and is not abundant there. The present results indicate that it will prey upon other gastropods in areas where it is more abundant and in this respect its feeding habits correspond to those of the other two *Conus* which are gastropod predators.

The Volutidae are neogastropods and these highly evolved prosobranchs are in the main carnivores, so it is not surprising that *Aulica vespertilio* like certain buccinids, thaids and fasciolarids was found to be a molluscan predator. It is more interesting to note the correspondence between the method employed by *A. vespertilio* and the unrelated mesogastropod, *Natica unifasciata* LAMARCK, 1822 (= *N. chemnitzii* PFEIFFER, 1840) to capture leaping gastropod prey (GONOR, 1965). Both species employ a "pouncing" movement with the propodium spread wide, and both manipulate the prey in the foot to the posterior portion, where it is then enclosed in a pocket and carried about before being eaten. Such close correspondence between two unrelated forms makes it probable that this capture and carrying method is a common feature of predatory prosobranchs which catch active clams and snails smaller than themselves. It provides a secure hold on the prey while allowing normal locomotion, and may function to kill or weaken the prey by cutting off its supply of oxygenated water, making subsequent feeding by the predator easier.

SUMMARY

Escape reactions of *Strombus gibberulus*, *S. luhuanus* and *Lambis lambis* (Strombidae) produced by the presence of *Aulica vespertilio* (Volutidae) and *Conus marmoreus* (Conidae) were observed in captured animals at Pulau Gaya and Pulau Mantabuan, North Borneo (118° 45′E, 4° 36′N). The strombids leap away from the predators more rapidly and further than they do in normal locomotion. The escape reaction is mediated by chemosensory detection of a substance released into the water by the predators, for water in which *C. marmoreus* had been kept also elicited the reaction. *Aulica vespertilio* and *C. marmoreus* captured and ate *S. gibberulus* when kept with them in containers overnight. Predation by *A. vespertilio* on *S. gibberulus* together with escape behavior of the *Strombus* were also observed in the field under undisturbed conditions. The avoidance response allows some individuals to escape when pursued by the predator. After detecting the *Strombus*, *A. vespertilio* rapidly pursues and then captures the prey by throwing the expanded propodium over it. The captured snail is then enfolded in the posterior part of the foot, and carried about before being eaten.

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